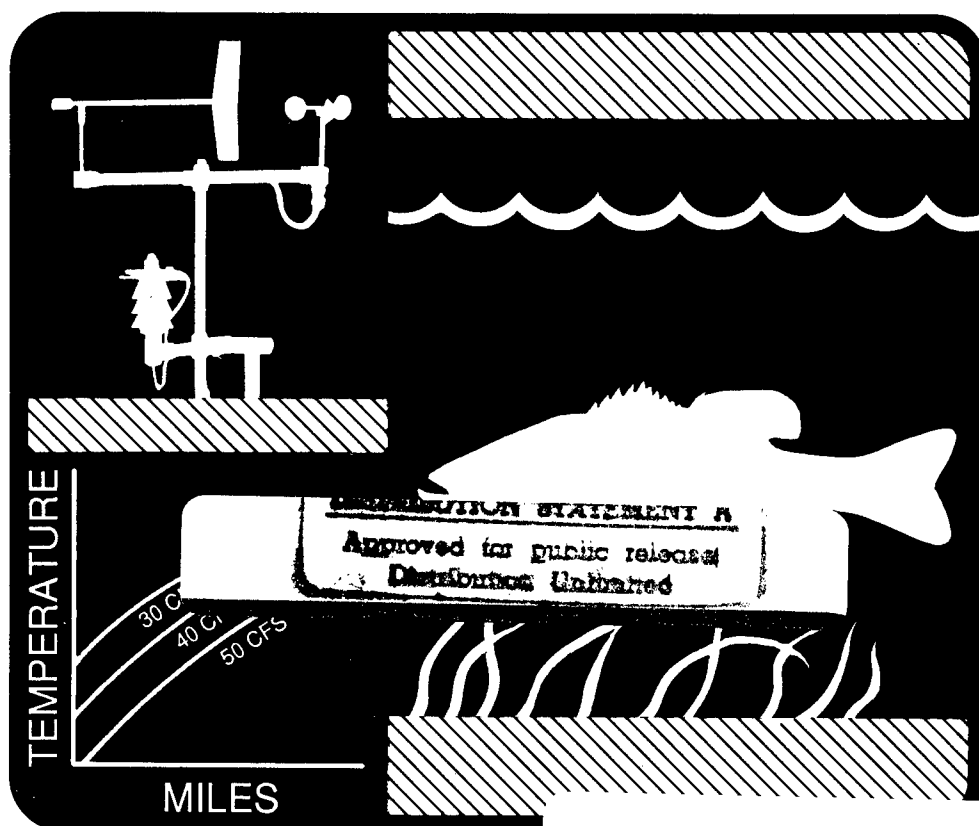# Evaluating Temperature Regimes for Protection of Smallmouth Bass

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Evaluating Temperature Regimes for Protection of Smallmouth Bass

By Carl L. Armour

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Carl L. Armour

U.S. Fish and Wildlife Service
National Ecology Research Center
4512 McMurry Avenue
Fort Collins, Colorado 80525-3400

Abstract. The success of smallmouth bass (*Micropterus dolomieu*) is affected by temperature regimes. Concepts are presented for evaluating the suitability of alternative temperature regimes through experimentally derived data, including ultimate incipient lethal temperatures and maximum weekly average, short-term maximum, and final preferendum temperatures. Also, concepts are described for basing evaluations on temperature tolerances for periods including spawning, egg and larval incubation, growth, and winter survival in the first year of life.

Key words: Alternative temperature regimes, *Micropterus dolomieu*, smallmouth bass, water temperature.

The smallmouth bass (*Micropterus dolomieu*) is an important sport fish species in the United States. Two subspecies are recognized: the northern smallmouth bass (*M. d. dolomieu*), which is native to the Great Lakes and adjacent regions, and the Neosho smallmouth bass (*M. d. velox*), which is native to northwestern Arkansas, northeastern Oklahoma, and southwestern Missouri (Hubbs and Bailey 1940; Ramsey 1975). This report applies mainly to the northern smallmouth bass.

In waters with controlled flows, survival of smallmouth bass is a concern because of potential for temperature changes. Temperature affects all poikilotherms (Fry 1967, 1971; Hutchinson 1976). Responses of fish to temperature changes can be affected by factors including size and sex, life stage, season, day length, water chemistry, disease, and genetic variation (Coutant 1970; Hutchinson 1976).

Smallmouth bass populations are affected by many variables (Fig. 1). Temperature in particular affects smallmouth bass directly by its influence on spawning, egg and larval incubation, and growth. Indirectly, it affects food availability, toxicity of waterborne substances, competition from sympatric species, oxygen saturation capacity of water, and biochemical oxygen demand, among others.

The potential effects of all variables that regulate smallmouth bass populations are incompletely known. However, enough is known about some direct effects of temperature to permit an assessment of probable impacts from alternative temperature regimes.

In writing this document, reliance was on existing literature. This precluded acquisition of new data and the field-testing of procedures for site-specific applications. It is hypothesized that procedures in this guidance are appropriate for evaluating the relative merits (rankings) of temperature
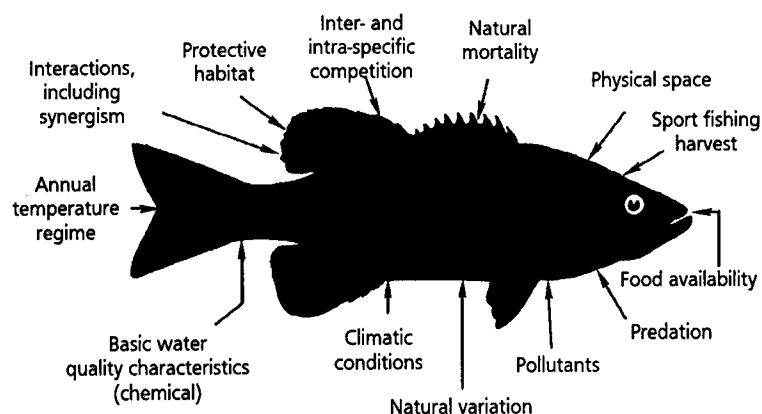
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Fig. 1. Variables that affect smallmouth bass (*Micropterus dolomieu*) populations.

regimes for smallmouth bass. Scientists are encouraged to challenge the validity of the assumption and to conduct studies to obtain information to improve the guidance.

Influences of Temperature on Smallmouth Bass

Water temperature is one of the most important environmental variables affecting smallmouth bass. For example, it influences geographic range, migrations to spawning sites, spawning date, nest-guarding by males, success of egg incubation, growth, and responses during the winter period, including feeding curtailment.

Smallmouth bass are sometimes classified as coolwater fish; however, they are tolerant to relatively high temperatures, and for this reason K. E. F. Hokanson (Duluth, Minn., personal communication) categorized them as warmwater fish. For example, in Tennessee, adult bass tagged with transmitters in summer remained in water exceeding 28.0° C, although cooler water existed in the thermally stratified, well-oxygenated reservoir (Bevelhimer and Adams 1991); in tank experiments, 74% of the fish selected a temperature of about 31° C when food was present. In Alabama, temperature experiments were conducted with age 0 fish; mean total length was 111 mm, and mean weight was 14 g. About 45% of the growth occurred at temperatures exceeding 29° C. The four temperature treatments were ambient and 3, 6, and 9° C above ambient. Temperatures ranged from 1

to 30° C for the ambient treatment compared with 10–38° C in the ambient plus 9° C treatment. In the ambient plus 9° C treatment, during the period of the highest temperatures, the fish had access to a refuge zone of 35° C. Growth occurred at temperatures above and below the 25–29° C range reported for optimum growth. Survival for a test period of 322 days was 87% for the ambient and 9° C above ambient treatments. Smallmouth bass in the 9° C above ambient treatment were exposed to temperatures of 35° C for 9 days. After 322 days, the net biomass of fish in the four treatments was not significantly different (Wrenn 1980). Stream conditions tolerated by smallmouth bass in Virginia included ambient temperatures up to 35° C (Stauffer et al. 1976).

In growth experiments in Tennessee with smallmouth bass and largemouth bass (*Micropterus salmoides*) fry, temperatures of 25–27° C promoted the fastest growth rates for both species (Coutant and DeAngelis 1983). The largemouth bass fry were in the 11.9–12.9-mm standard length range at the beginning of the experiments in early May, and the smallmouth bass were in the 10.1–12.5-mm range. The temperature for maximum growth of largemouth bass was about 27° C, compared with 25–26° C for smallmouth bass. Coutant and DeAngelis (1983) thought that growth rates for cool years for both species would probably be comparable.

Streams known for high-quality smallmouth bass populations generally have the following habitat characteristics: cool, nonturbid water, abundant shade and cover, deep pools, and substrates composed of gravel and larger material

(Edwards et al. 1983). Smallmouth bass are commonly successful in eastern mid-order streams that are managed for "put and take" trout fisheries, which usually have these characteristics.

McClendon and Rabeni (1987) evaluated 32 variables thought to influence smallmouth bass populations in a Missouri stream. The highest abundance and biomass correlated with relative amounts of boulders and cobble, availability of undercut banks, and the presence of vegetation. Relative weight (an index of fish condition) correlated positively and best with maximum summer water temperatures (mean = 24° C, range = 14.5–29.7° C) and crayfish abundance (mean = 62,000/ha, range = 21,000–213,989/ha).

Evaluating Regimes with Temperature Tolerance Data

Compiled thermal-table information with regression coefficients (as in Brungs and Jones 1977) is unavailable for smallmouth bass. However, other information from temperature studies (Table 1) can be used in evaluating temperature regimes.

I interpreted from Wrenn (1980) that the upper ultimate incipient lethal temperature (UUILT) for juveniles and adults is 37° C. This is the highest temperature at which tolerance does not increase with increasing acclimation temperatures. The

Table 1. *Temperature response criteria reported for smallmouth bass* (Micropterus dolomieu).

Criterion[a]	Value (° C)	Reference and fish source	Comment
Estimated UUILT for juveniles	37	Wrenn (1980), Carbon Hill National Fish Hatchery, Alabama	Although the author reported 37° C to pertain to the UILT, I interpreted that he meant UUILT
MWAT for adequate juvenile and adult growth	32–33 Alabama	Wrenn (1980), Carbon Hill National Fish Hatchery, 6, and 9° C above ambient	Responses were studied at treatments of ambient and 3,
STM for juveniles and adults for summer growth	35	Wrenn (1980), Carbon Hill National Fish Hatchery, Alabama	Survival in a channel at ambient +9° C was 87%; maximum water temperatures period approximated 35° C for 70 days in the channel and the minimum temperature was 35° C for 9 days; age 0+ fish were held for 322 days in the experiments
STM for embryo development	23	Wrenn (1984), Tennessee River	The value was cited as being conservative; the author believed that a maximum of 26° C is more realistic for spawning and embryo protection
FP	30.3–31.5	Cherry et al. (1977), New River, Virginia area	Seined fish of unreported sizes were used in the experiment; the best statistical fit was for 30.3° C; two values (i.e., 28 and 31° C) of other researchers were reported
FP	30.8	Stauffer et al. (1976), New River, Virginia	Data were from a stream survey; smallmouth bass were sampled at temperatures up to 35° C
FP for adults	27	Hokanson (personal communication); multiple sources	The value was the mean for the range of 20.3–33° C

[a] UUILT = upper ultimate incipient lethal temperature; MWAT = maximum weekly average temperature; STM = short-term maximum; FP = final preferendum.

maximum weekly average temperature (MWAT) reported (Wrenn 1980) for juveniles and adults is 32–33° C. An MWAT value is a temperature between the physiological optimum and the UUILT (Wismer and Christie 1987).

Cherry et al. (1977) reported a range of 30.3–31.5° C for the final preferendum (FP); other authors (Table 1) reported values ranging from 27 to 30.8° C. The FP is the temperature that fish will ultimately select regardless of acclimation temperature (Giattina and Garton 1982). If an FP temperature zone is available, fish should be most abundant there, assuming that adequate food is available and that there are no other habitat problems (e.g., pollution). The physiological significance of an FP temperature is that it potentially corresponds to the temperature at which key physiological, biochemical, and life history activities are optimal (Beitinger and Fitzpatrick 1979).

A short-term maximum (STM) of 35° C for growth was reported for experimental results with Alabama hatchery fish (Table 1; Wrenn 1980). The experiment involved subjecting fish to four temperature treatments of ambient, and ambient plus 3, 6, and 9° C for 322 days in outdoor channels. In the ambient plus 9° C channel, maximum temperatures were near or above 35° C for 70 days, and the minimum temperature was 35° C for 9 days.

Wrenn (1984) studied additional effects of the four temperature regimes described above on the survival of smallmouth bass eggs and larvae. Survival rates from the egg stage to the time fry emerged from the nest approximated 90% for each of the four treatments. Based on results of the study, the recommended limit for spawners and embryo protection was about 26° C.

If temperature information can be simulated for alternative flow regimes, then temperature response information such as that given here can be used to evaluate the relative merits of the thermal regimes for smallmouth bass. For example, the STM for incubating embryos might be the concern (Table 2). Of the three hypothetical temperature regimes, alternative A would be recommended to ensure successful embryo development. The same type of comparisons could be made for UUILT, MWAT, and FP values for appropriate life stages.

Table 2. *Application of the short-term maximum (STM) criterion for incubating smallmouth bass embryos in evaluating alternative temperature regimes.*

	Alternative temperature regime		
	A	B	C
Hypothetical short-term temperature (° C) during the egg incubation period	21.1	25.6	31.1
STM of 23° C exceeded for embryos?	No	Yes	Yes

Evaluations Based on Life Stage and Activity Requirements

When alternative temperature regimes are evaluated, emphasis must be on their capabilities to fulfill requirements for key activities and life stages of smallmouth bass (Table 3). When using Table 3 for a site-specific analysis of the suitability of temperature regimes, professional judgment must be exercised in selecting the most appropriate values for a specific geographic site. Important considerations for year-class success include the suitability of a regime for spawning, embryo development on the nests, and summer growth of fry (Fig. 2). Rates of development are important because they may influence susceptibility of a life stage to mortality from other factors, including predation. For example, within the acceptable range for hatching, there is an inverse relation between temperature and hours until hatching (Fig. 3). Rapid development reduces the time period when nests are susceptible to destruction by predation or weather changes. Information on mortality rates for the first year of life is sparse (Table 4). However, in Missouri creeks there was a 98.5% mortality rate by fall (Pflieger 1966) for young from the first spawning period, compared with an 83% mortality rate from eggs to the fall fingerling stage in a Michigan lake study (Clady 1975). Some critical life stages and the thermal requirements applicable to them are discussed below.

Table 3. *Temperature data for smallmouth bass compiled from the literature.*

Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Spawning migrations			
Adults return to stretches of river abandoned in the fall at 15° C	N	Langhurst and Schoenike (1990), Embarrass River, Wisconsin	The fish overwintered elsewhere and repopulated a 5-km reach of the river vacated in fall
Males migrate to spawning sites when temperatures approximate 15.6° C	N	Coble (1975), source not revealed	Males construct nests and spawning may occur immediately or there may be a week or more of delay, depending on water temperature and availability of ripe females
Initiated when minimum water temperatures exceed 15.6° C	N	Cleary (1956), Iowa streams	A freshet preceded migrations
Spawning occurs			
15–18.3° C range	N	Hubbs and Bailey (1938), assumed to be throughout the smallmouth bass range	Approximately 15° C when temperatures elevate steadily and near 18.3° C if elevations are relatively sudden
12.8–15.6° C	E	Henderson and Foster (1956), Columbia River Slough near Richland, Washington	Temperatures in the main river channel ranged from 7.2 to 10° C; when this water entered the slough and temperatures were reduced to 12.2° C, no bass were observed
19–20° C	E	Wrenn (1980), Carbon Hill National Fish Hatchery, Alabama	Studies were in outdoor channels; spawners were age 1 fish
Initiated at 18.3° C	N	Latta (1963), Waugoshance Point, Lake Michigan	The temperature was expressed as the mean, defined as the average of the daily maximum and minimum temperatures; means were in the 15.6–20.6° C range during all of the spawning season; the 18.3° C value was reported for nesting that is assumed to include spawning
15–21° C	N	Shuter et al. (1980), Baie du Doré and Lake Opeongo, Ontario	Egg-laying suppressed at temperatures <14.2° C and >28° C; fish resume spawning when temperatures reenter 15–27° C range; water temperatures reached and exceeded 15° C before the peak of spawning; mortality of eggs and larvae is 100% if daily mean temperatures drop below 10° C or exceed 30° C; there is no temperature-related mortality in the 15–27° C range; 15° C is the minimum temperature for the complete survival of larvae

Table 3. *Continued.*

Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Spawning occurs (continued)			
Onset observed at 11.6° C	N	Phelan and Philip (1990), St. Lawrence River	At the peak of spawning, the temperature was 15° C; the temperature during the latest date of spawning was 17.6° C
When temperature decreases to 12.8° C, nest preparation and spawning cease, resume at 13.9° C	N	Meehan (1911), unspecified Pennsylvania waters	Eggs were killed when water temperatures dropped to 7.2° C
Spawners occupied water in 20–22° C range	N	Gerber and Haynes (1987), tributaries of Lake Ontario, Canada	Smallmouth bass rarely observed in water exceeding 25° C during the summer; this was assumed to include the post-spawning season
Temperatures much lower than 15.6° C cause a cessation of nest building by males	N	Hubbs and Bailey (1938), assumed to be throughout the range of smallmouth bass	Vacating of a nest by a male usually causes loss of all eggs and fry
Bulk of spawning in 15.6–21.1° C range with peak at 17.8° C	N	Watson (1955), Maine bass in general	Nest-building begins at approximately 12.8° C; at Big Bear Lake it began at 14.4° C
Spawning occurs when temperatures exceed 15.6° C	N	Harlan et al. (1987), Iowa streams	Spawners move up larger streams in early May
Approximate 15–21.1° C range	E	Rawson (1938), Waskesiu Lake, Saskatchewan was location of study but the fish were from the north channel of Lake Huron	Fish were in screened enclosures; temperatures were assumed to be the average of daily maximum and minimum temperatures; spawning was preceded by a temperature rise from 12.8 to 15.6° C
A water temperature rise to approximately 15.6° C precedes spawning	E	Rawson (1945), Prince Albert Park, Saskatchewan	Brood fish were held in rearing enclosures and were observed; in 1936, the range of spawning temperatures was approximately 15–20° C compared with 14.4–18.3° C in 1939, 15–20.6° C in 1941, and 15–18.3° C in 1942; temperatures were assumed to be the average of daily minimum and maximum temperatures
First occurrence of nesting and spawning observed at 18.5° C	N	Winemiller and Taylor (1982), Indian Creek, Ohio	Authors believed that unsuccessful male spawners were relatively small, nondominant fish
Nest construction by males and spawning followed several days during which maximum water temperatures exceeded 15.6° C	N	Pflieger (1966), Little Saline Creek, Missouri	Daily maximum temperatures ranged from 18.9° C early in the season to 26.7° C several days near the end of the season; daily minimum temperatures ranged from 12.2 to 17.8° C; diurnal fluctuations ranged from 3.3 to 7.8° C

Table 3. *Continued.*

Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Spawning occurs (continued)			
Larger males spawned with exposure to fewer degree-days than smaller males	N	Ridgway et al. (1991), Lake Opeongo, Ontario	Degree-days are those with average temperatures higher than 10° C; the same pattern appeared for females; it was hypothesized that large males overwinter with a lower energy deficit and can breed earlier than smaller males, and that large males allocate more energy to reproduction than to growth earlier in the season than small males
Peak egg deposition occurred at 18–22° C, temperatures below 10° C and above 30° C are usually lethal to spawns	E	Wrenn (1984), Tennessee River, Tennessee	Egg incubation success was studied for three temperature regimes (3, 6, and 9° C above ambient); survival from egg to emergent fry approximated 90% for the regimes; Wrenn (1984) concluded that a maximum weekly average temperature of 26° C during the spawning season is suitable for survival of eggs and larvae
Spawning occurred when daily mean temperatures ranged from 12.5 to 23.5° C	N	Graham and Orth (1986), tributaries and main stem of New River in West Virginia and Virginia	Spawning was sharply curtailed when temperatures reached 25° C
Spawning observed at temperatures ranging from 13.3 to 22.5° C	N	Vogele (1981), Bull Shoals Lake, Arkansas	Free-swimming fry were guarded by the male parent for approximately 4 weeks
Usually begins at 12.8° C	N	Newell (1977), New Hampshire	The author reported that spawning is usually completed when the water temperature is 21.1° C
Lower and upper spawning thresholds are 12.3 and 27.2° C	L	Hokanson (personal communication), fish source unspecified	The values are the lower average temperatures for spawning and embryo development
Spawning occurred when daily temperatures ranged from 11.7 to 20° C	N	Brown (1960), Little Miami River, Ohio	Nesting occurred in the daily 9.4–21.1° C range; the author reported that bass in the Toledo Aquarium spawn at an average of 21.1–22.2° C with a range of approximately 20–23.3° C

Table 3. *Continued.*

Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Spawning occurs (continued)			
26° C is the monthly or seasonal maximum limit for spawning and embryo protection	E	Wrenn (1984), Tennessee River, Tennessee	Age 1+ fish were stocked in four temperature regimes—ambient and treatments of 3, 6, and 9° C above ambient; spawning occurred successfully at 22° C; the author stated that a maximum of 17° C for successful spawning and 23° C for embryo survival (Brungs and Jones 1977) is conservative
22.8° C was the water temperature at which eggs were initially observed	N	Smitherman and Ramsey (1972), Mammoth Spring National Fish Hatchery, Arkansas	Fish were stocked in earthen ponds; the effective spawn (resulting in fry production) was at 23.9° C, reported in a table (in the text, 25.6° C was reported); temperatures were taken at water surface
Nest-building and spawning occurred in the 15–18° C range	N	Turner and MacCrimmon (1970), Tadenac Lake, Ontario	Egg incubation lasted 4 days at temperatures of 15.3–18.2° C; temperatures were assumed to be average of daily maximum and minimum recordings
Began by time field work was initiated and daily temperature was in the 17.2–21.1° C range	N	Stone et al. (1954), Millen Bay, Lake Ontario	The observation was on 15 June 1948; the authors concluded that spawning occurred during the first 2 weeks of June; additional nests were found after June 15
12.5–23.5° C	N	Graham and Orth (1986), New River in Virginia and West Virginia	The mean daily water temperature was the most important variable in determining time of spawning
Occurred at a range of 19.4–21.1° C for the first spawning	N	Surber (1939), Cacapon River and South Branch of the Potomac River in West Virginia, and the Shenandoah River in Virginia	The observations were for the first spawning, from 28 April to 2 May; a second spawning occurred at 23.9° C in the Cacapon River and 25° C in the South Branch of the Potomac; the respective dates for the second spawning were 10 June and 14 June
Egg and larvae incubation			
Survival for eggs to the hatch stage is favorable at 15–25° C	E	Kerr (1966), Ontario fish	Research was performed in the laboratory, where hatching success and incubation temperatures were studied; hatching success ranged from 73 to 98%; the peak occurred at 20° C, at which the average percent hatch for two samples was 93.5%

Table 3. *Continued.*

Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Egg and larvae incubation (continued)			
18.3–21.1° C temperatures observed during incubation and hatching phases	N	Rawson (1938), Waskesiu Lake, Saskatchewan was location of study but fish were from the north channel of Lake Huron	Eggs were incubated in June in a cellar at 14.4–15° C and hatched in 4 days; it took 3 weeks to attain a post-hatch development stage that took 2 weeks at normal temperatures
Survival of eggs and fry is 0 if the daily mean temperature drops below 10° C or elevates above 30° C	N, E	Shuter et al. (1980), Lake Opeongo, Ontario	Conclusion based on data from Kerr (1966) and observations of Shuter et al. (1980)
Mortality of embryos occurred when water in the 17.8–20° C range was subjected to a sudden rise to 23.1° C	E	Tester (1930), Lake Nipissing, Ontario	Information is for embryos near hatching stage
Fry hatched from eggs at 15.6–23.9° C in sloughs	N	Henderson and Foster (1956), Columbia River sloughs, near Richland, Washington	Hatching occurred in the sloughs in July or August when temperatures were in the range
Incubation range from 10 to 23.9° C; constant temperature is not lethal and normal temperature alterations within the range are tolerated	E	Webster (1948), Cayuga Lake, New York	Reported that, in a river, temperatures ranged from 10 to 26.7° C during the spawning and nesting season, and the daily mean fluctuation was 5.8 ± 1.9° C; eggs exposed to experimental temperatures had been developing at 18.3° C and the change to different temperatures occurred within a half-hour period
Ranges from 14 to 21° C had no adverse effects on eggs or larvae	N	Neves (1975), South Branch Lake, Maine	The range is for mean daily temperatures, defined as the average of the daily maximum and minimum temperatures
Egg mortality occurred at approximately 14.4° C	E	Rawson (1945), Waskesiu Lake, Saskatchewan	Temperatures declined to approximately 14.4° C in 1939 and the 14.4–16.7° C range in 1942, when mortality was observed; temperatures assumed to be average of daily maximum and minimum temperatures, observations made in spawning beds
For successful egg development, a period of 2–3 weeks is required with temperatures of approximately 18.3° C and higher	E	Rawson (1945), Waskesiu Lake, Saskatchewan	General statement based on observation of nests in enclosures; temperature criterion assumed to be daily mean
Virtually all eggs hatched at a constant temperature of 22° C	E	Peek (1965), Arkansas Game and Fish Commission Hatchery at Centerton	After 24 h from hatching, fry had reached dark-eyed stage

Table 3. *Continued.*

Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Egg and larvae incubation (continued)			
Declining minimum temperatures approximating the 10–12° C range and highs of about 30.6–31.7° C are lethal to embryos and newly hatched fry	N	Brown (1960), Little Miami River, Ohio	When temperatures dropped to the reported range, advanced fry developed in 1 nest out of 71; mortality included influences from indirect effects
Eggs and young-of-year died if temperatures dropped below 14° C during the interval from fertilization and next rise	N	MacLean et al. (1981), Lake Opeongo and Baie du Doré, Ontario	Mortality occurred when a cold front caused cold hypolimnetic water to enter the spawning area
Nest abandonment by males			
Temperature dropped from 16.1 to 12.2° C in sloughs where spawning occurred	N	Henderson and Foster (1956), Columbia River sloughs near Richland, Washington	One week after abandonment, the temperature was 12.2° C and eggs were coated with fungus
Males desert nests when the water temperature drops to 10–15° C and lower	N	Latta (1963), Waugoshance Point, northern Lake Michigan	Eggs were eaten by predators after males left
Temperature falls from 18.3° C to slightly below 10° C	N	Webster (1954), Cayuga Lake, New York	Unguarded nests can produce fry but it is possible that the survival rate is lower than in guarded nests
Nest abandonment occurs if temperatures drop to 15.6° C and lower for a prolonged period	E	Rawson (1945), Waskesiu Lake, Saskatchewan	Temperatures assumed to be average of daily maximum and minimum values; nests were in spawning pens; desertion results in death of eggs and, to a lesser extent, death of unrisen fry
Occurred when temperature drops below 10° C	N	Lyndell (1902), culture ponds in Michigan	Abandonment resulted in the death of eggs and fry; for the production of young-of-year fish, the recommended temperature range is 18.9–23.9° C
Growth			
Optimum temperature for juveniles is 26° C	L	Schlesinger and Regier (1983), general statement	Derived for maximum ration conditions that are probably rare in nature
Maximum growth for juveniles is approximately 26° C, fish held at 35° C had negative growth	E	Horning and Pearson (1973), Osage Catfisheries, Missouri	Results based on constant temperatures with tests on fish weighing 5.1–70.8 g (mean = 29.4 g); tests were for constant temperatures of 16–35° C; food was unlimited

Table 3. *Continued.*

| Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Growth (continued)			
A mean weekly average of 32–33° C allows satisfactory growth of juveniles and adults	E	Wrenn (1980), Carbon Hill National Fish Hatchery, Alabama	Fish were 0+ at stocking in experimental channels and averaged 11 cm total length; it was assumed that food was not limited; the experiment was conducted at four temperature treatments (ambient and ambient +3, 6, and 9° C)
Maximal first-month growth of fry occurred at 25–26° C	E	Coutant and DeAngelis (1983), Cohutta National Fish Hatchery, Georgia	Test temperatures (constant) ranged from 15.2 to 27.3° C; food was not limited
Temperature decline from 22.9 to 14.7° C over a 3-day period adversely affected growth of body parts and total length of fry	N	Doan (1939), Lake St. Clair, Ontario	Measurements were in June; temperatures were average of daily maximum and minimum values at nest
Maximum safe temperature limit for growth of fingerlings, juveniles, and adults at 29° C	N, E	Horning and Pearson (1973), Osage Catfisheries, Missouri	Conclusion based on experimental results of authors and their evaluation of information in the literature; food was not limited
An annual thermal sum degree value of less than 1,000 units was attributed to diminished population success	N	Pettit (1976); Clearwater River, Idaho	An annual thermal sum degree value is the sum of mean temperature for days when the 10° C degree-day level is exceeded for a period from July through September; Coble (1967) reported that, predominantly, for average annual length increments of 2.5 cm or more for adult fish, the sum exceeded 1,000 units
Activity in general			
Approximately 10° C is the temperature at which activity diminishes with a lowering trend and resumes with rising temperatures	N	Hubbs and Bailey (1938), assumed to apply throughout the range of the smallmouth bass	Smallmouth bass hibernate in winter when growth stops or activity is greatly reduced
Fish become torpid in the the range of about 4.4–6.1° C	NS	Coble (1975), source not revealed	The fish rarely feed at this temperature range
Fish tend to enter rock substrate and remain when temperatures are <7.8° C	E	Munther (1970), Snake River, Idaho	Fish in tests were young-of-year ranging from 7 to 10 cm total length
Few bass caught until water warms to 10–15.6° C range	N	Watson (1955), lakes in Maine	Water reached the range in late May or early June
Move to wintering habitat at temperatures <15.5° C	N	Munther (1970), Snake River, Idaho	Fish were in still, rocky pools at least 4 m deep when studies occurred in late fall
Migration to winter habitat can initiate at 15.6° C and is pronounced at 10° C and lower	NS	Coble (1975), general statement	Fish move to zones that are dark and devoid of current (e.g., crevices between rocks, holes, caves, hollow logs)

Table 3. *Continued.*

| Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Activity in general (continued)			
Fish feed at temperatures exceeding 10° C	E	Munther (1970), Snake River, Idaho	Fish were young-of-year about 7–10 cm total length
At 7.1° C age 0 captive fish consumed virtually no food	E	Oliver (1977), White Lake, Ontario	Tests were in aquaria; the fish were fed trout food
Age 2 and older fish initiated winter migration when temperatures fell below 16° C	N	Langhurst and Schoenike (1990), Embarrass River, Wisconsin	At temperatures below 4.4° C, age 2 and older fish were not in the study area and were assumed to have migrated to overwintering sites; adults (fish >280 mm) migrated sooner than subadults (200–250 mm fish); no evidence was found that smaller fish migrated
At temperatures below 10° C most fish were in a hibernating stage	E	Oliver (1977), citing unpublished data of J. C. MacLeod, Lake Opeongo, Ontario	Oliver (1977) reported that bass in an Ontario study virtually stopped feeding at 7.1° C; the fish were young-of-year from White Lake, Ontario
At temperatures of 6.5–8° C fish had not fed for several weeks	N	Keast (1968), Little Cataraqui Creek, Ontario	Stomachs were shrunken and drawn forward in the body cavity
Other			
Seasonal selection temperatures (° C) were 29–31 for underyearlings (UY) and 30–31 for adults (AD) in summer, 26–30 UY and 21–27 AD in fall, 24–28 UY and 13–26 AD in winter, and 22–28 UY and 18–26 AD in spring	E	Barans and Tubb (1973), western Lake Erie near South Bass Island, Ohio	Acclimation was at ambient lake temperatures at time of seasonal tests
At times, sunning fish selected 26.7° C	N	Munther (1970), Snake River, Idaho	Fish selected shallow backwater areas; sizes of fish unstated
Average summer temperature where fish were observed was 21.4° C	N	Hallam (1959), Ontario streams	Fish sizes not specified; at sampling time, one water temperature was recorded and ranges were not
After spawning and water temperatures dropped from 10 to 15.6° C, eggs became heavily infested with fungus	N	Cleary (1956), Iowa	Air temperatures dropped from 23.9 to 11.1° C in a day and remained low for 10 days
Range of approximately 20.3–21.4° C where fish were observed in mid-summer	L	Ferguson (1958), data for Nebish Lake, Wisconsin and streams in Ontario	Assumed to be preferred temperatures; ages of fish unspecified; final preferendum for laboratory studies was 28° C

Table 3. *Continued.*

Temperature data for activity and life stage	Observation[a]	Reference and fish source	Comments
Other (continued)			
Northern latitudes where smallmouth bass predominate seldom have mid-summer temperatures exceeding 26° C	NS	Coutant and DeAngelis (1983), general statement	Temperature alone may not be the primary factor in determining the relative abundance of smallmouth bass in the presence of largemouth bass
Most adult fish vacated spawning area when temperature approximated 25° C	N	Robbins and MacCrimmon (1977), Pefferlaw River, Ontario	Fish were spent spawners from Simcoe Lake; remaining adults vacated after temperatures elevated to 29° C
Optimum growth of juveniles occurred at approximately 28° C	E	Peek (1965), Arkansas Game and Fish Commission Hatchery at Centerton	The temperature was the average of the preferred temperature for most fish for three test ranges (17–31.4, 20.8–35, and 17.8–38° C); Peek (1965) concluded that bass fingerlings tend to choose the temperature (28–29° C) at which growth is maximum
33–35° C are summer temperatures that fail to form a thermal barrier for migrations	E	Wrenn (1976), Tennessee River, Tennessee	Movements of tagged fish were studied in a thermal plume from a power plant; the author documented preferred temperatures by season
Cold shock mortality occurred when there was a sudden change from 26.7 to 2.2° C	N	Silverman (1971), Susquehanna River, Pennsylvania	The fish were in a thermal discharge that was shut off
During lighted conditions, the highest temperature selected by smallmouth bass was 30.1° C, compared with 28.3° C in darkness	E	Reynolds and Casterlin (1978), source not revealed (assumed to be Pennsylvania stock)	There were alternating periods of 12 h of light and 12 h of darkness; for largemouth bass (*Micropterus salmoides*) the highest selected temperature during light periods was 29.1° C, compared with 29.5° C in darkness; the authors suggested that the behavioral difference relates to niche segregation triggered by circadian rhythms

[a] N = observed under field conditions; E = experimental; L = analysis of literature by cited author; NS = not specified.
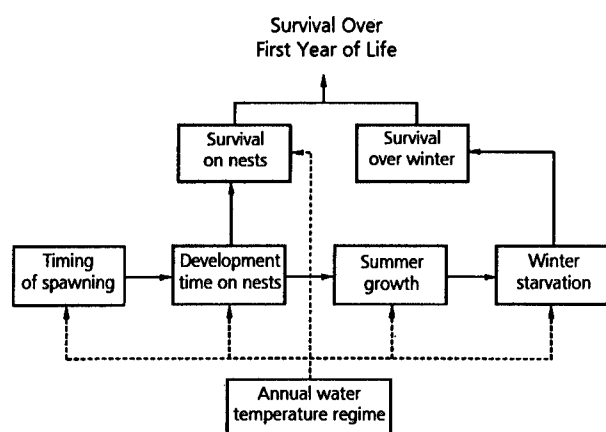
Fig. 2. Conceptual model of the influences of temperature on first year survival of smallmouth bass (Shuter et al. 1980).
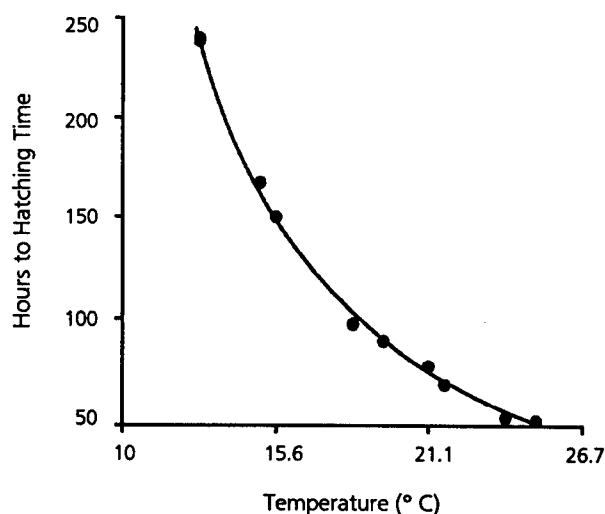
Fig. 3. Temperature versus hatching time for smallmouth bass eggs, assuming at least 50% survival (from Webster 1948).

Table 4. *Mortality (%) data reported for smallmouth bass from the egg stage through the first year of life.*

Egg to hatching	Egg to fry	Egg or fry to fall fingerlings	Fingerling through first year	Reference, fish source	Comment
5.9	6.1	98.5[a]	NR[b]	Pflieger (1966), Little Saline, Bois Brule, and Big Saline creeks, Missouri	The value for eggs is the mean for five nests; the range was 0 to 44.7% with $n = 17$; an estimated 80,300 fry (two nestings) were produced in 1.6 km of stream; broods of fry were produced in approximately 33 of 41 nests
NR	72.4	NR	NR	Latta (1963), Waugoshance Point, Michigan	The estimate is for values from two nests for which eggs were counted and three for which fry counts were made
37	NR	NR	NR	Vogele (1981), Bull Shoals Lake, Arkansas	The mean number of eggs and larvae for nest was 7,757 and 2,855, respectively
67.5–74.2	NR	83[c]	86	Clady (1975), Katherine Lake, Michigan	Larvae information is for the past larvae stage; annual survival was documented for 3 years from the egg to the fall fingerling stages; the fingerling survival information was based on numbers of fish measured after age 1 for two year classes

[a] Reported as young of the nesting period.
[b] NR = not reported.
[c] From eggs.

Nest Abandonment by Males

An important factor in the production of young-of-year fish is nest and fry-guarding by males after spawning (Surber 1943; Rawson 1945; Latta 1963). If temperatures drop below approximately 14° C, males may abandon nests. Abandonment by the male for any reason can cause young-of-year mortality. For example, sunfish predation on smallmouth bass fry was documented for a Missouri stream (Pflieger, 1966) following nest abandonment. One bluegill consumed 39 fry in the absence of the male on the nest, and sunfish were observed attempting to feed on dispersing fry, indicating that fry may be particularly vulnerable to predation when nest abandonment occurs. Neves (1975) observed that three nests without male guards produced about 1,000 fry compared with 3,943 fry per guarded nest. Webster (1954) observed male abandonment in a New York lake when temperatures dropped from 18.3° C to about 10° C; fry were produced in 12 abandoned nests, but Webster thought survival from the egg to the black fry stage would be higher in guarded nests. In a study of Iowa streams (Cleary 1956), fingerlings were produced, but the guarding of newly hatched fry was not observed.

If eggs and fry from the first spawning are destroyed because of low temperatures, respawning and fry production is possible when water temperature increases (Fig. 4; Rawson 1945). A second spawning occurred in two West Virginia streams a month after the first spawning (Surber 1939). The first spawning was unsuccessful because it was followed by a period of cool weather and elevated water levels. Almost all fry from the first spawning

were destroyed. The average water temperatures for the first and second spawning were 20 and 24.4° C, respectively. After fry were produced in South Branch Lake in Maine from a first spawning, water temperatures dropped to about 16.1° C, and there was a second spawning when temperatures rose to about 17.8° C (Neves 1975).

Another phenomenon is the inducement of earlier-than-normal spawning in response to higher temperature regimes. In Alabama experiments (Wrenn 1984) with four temperature regimes, the spawning peak (22 March) for the highest temperature regime of ambient plus 9° C was 25 days in advance of the peak (16 April) for the ambient regime. Spawning occurred at 22° C in the ambient plus 9° C treatment, compared with 17.6° C in the ambient treatment.

The period of nest and fry guarding by males varies, but, regardless of the time, if temperature changes cause nest abandonment there can be young-of-year losses. One period of nest and fry-guarding lasted for at least 40 days, including 26 days after fry swarmed above the nest and complete dispersal occurred (Tester 1930). A guarding period in an Ontario lake lasted 19 to 28 days after hatching and dispersal were completed (Turner and MacCrimmon 1970). Guarding continued for 2 to 5 days after fry dispersal in a Missouri stream (Pflieger 1966). Guarding extended to 4 weeks after fry schools were observed in Bull Shoals Lake in Arkansas (Vogele 1981).

Unless site-specific data are available to justify a different conclusion, temperatures resulting in nest abandonment at any time from spawning to the complete dispersal of fry could be considered 100% lethal to offspring.
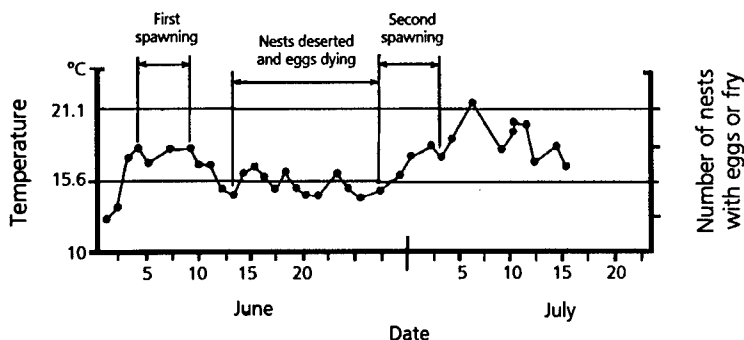

Fig. 4. First spawning, nest desertion by males, and respawning of smallmouth bass in Narrows Bay, Saskatchewan (from Rawson 1945). More nest desertion occurred (for unknown reasons) after the second spawning when the high temperatures approximated 21.8° C, compared with the low of 19.2° C.

Prediction of Spawning, Hatching Time, and Rising from Nests

One challenge in evaluating alterative temperature regimes is the designation of specific periods for important life stages or activities. Periods of special concern are those for spawning, hatching, and rising from the nest. The duration of these periods is temperature dependent, and empirical information pertaining to temperature versus days for hatching through nest abandonment has been documented (Table 5).

Usually, the spawning period for a specific location can be estimated through communications with qualified experts and reference to historical records. However, if the period must be estimated solely from temperature data, one option is to use the degree-day approach (Shuter et al. 1980). This approach requires estimation of the number of degree-days (days with average temperatures exceeding 10° C) to which spawners are exposed after the 15° C level is initially reached in the prespawn period. With this information, the peak time of spawning can be estimated. For example, if 40 degree-days accumulated by 1 May, the date on which the 15° C level initially occurred, the estimated peak of spawning would be about 7 May (Fig. 5).

Alternatively, equations developed by Shuter et al. (1980) can be used to estimate the time for egg laying (D), the time from fertilization to hatching (T_{SH}), and the time from hatching to rising (T_{HR}) of fry from nests. Equation 1 can be used to estimate days (D) until egg laying.

$$D = 8.0 - 0.55d \quad (1)$$

where

d = estimated number of degree-days above 10° C accumulated by the date that average temperatures entered the preferred range of 15-27° C; for example, if the preferred temperature range exists and d = 10 days, then D = 8.0 - 0.55(10) = 2.5 days.

Equation 2 can be used to estimate the time from fertilization to hatching (T_{SH}).

$$T_{SH} = 83.2e^{-0.1606T} \quad (2)$$

where

Table 5. *Temperature versus time reported for smallmouth bass egg hatching through nest desertion by fry.*

Days	Temperature (° C)	Reference
Hatching		
7.0	14.4-15.6	Vogele (1981)
5.0	17.8-18.6	
3.9	Mean = 19, range of daily means = 18.2-20.0 (E)[a]	Neves (1975)
3.5-5.4	15.1-21.1	Rawson (1945)
4.0	15.2-18.2	Turner and MacCrimmon (1970)
6.0	15.6-18.3	Vogele (1981)
6.0	16.7-17.5	
2.2	25.0	Webster (1948)[b]
2.3	23.9	
2.9	21.7	
3.2	21.1	
3.8	19.4	
4.1	18.3	
6.3	15.6	
7.0	15.0	
9.9	12.8	
9.8	12.8	
Hatching to rise		
11.0	20-21.5 (E)	Neves (1975)
8.0-11.0	11.3-18.2 (E)	Turner and MacCrimmon (1970)
3.0-7.0	18.3-23.3	Inslee (1975)
4.1-8.4	17.2-21.1	Rawson (1945)
12.0	12.2-23.1	Tester (1930)
8.0-11.0	17.2-19.5	Turner and MacCrimmon (1970)
Egg deposition to nest desertion by fry		
18.9	15.2-23.8 (E)	Turner and MacCrimmon (1970)
10.3-15.0	17.2-21.1 (E)	Rawson (1938)
8.0	15.3-16.4	Vogele (1981)
6.0	18.3-21.1	
14.0-15.0[c]	15.6-23.9	Pflieger (1966)

[a] E = estimated from the cited data.
[b] Data for time at which 50% of eggs hatched.
[c] Information for first spawning. For the second spawning, fry were dispersed by 10-12 days. Mean temperatures were the average of daily maximum and minimum temperatures.
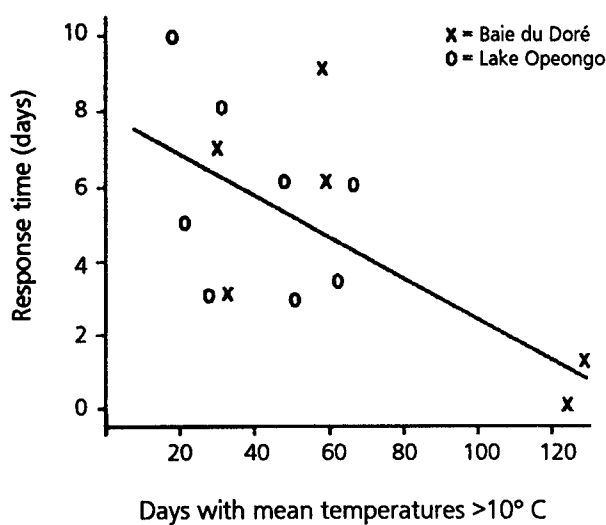
Fig. 5. Relation between degree-day accumulations and days to initiation of spawning. Degree-days are days with average temperatures greater than 10° C following the date on which temperatures initially reach 15° C during the prespawning period (from Shuter et al. 1980).

T = the average postspawning temperature (° C) for the incubation period.

Equation 3 can be used to estimate the period from hatching to rising of fry from the nests.

$$T_{HR} = 134e^{-0.1606T} \qquad (3)$$

The equations can be applied to estimate periods for which adverse temperatures could threaten year-class success at a critical early life stage. Suppose, for example, that there is concern that adverse temperatures could induce nest abandonment by males and hence loss of eggs and larvae. Assuming that average temperatures for alternative flow regimes could be estimated and that the maximum and minimum temperatures would be within tolerance limits for satisfactory development, the equations could be used to estimate the period from egg laying to rising of fry from the nests (as in Table 6). Also, the duration of the prewinter growth period (when temperatures exceed 10° C) could be estimated. In the example, it would be about 30 days longer for regime B than for regime A or C.

If temperature-induced mortality of eggs, larvae, and fry is the concern, equations developed by Shuter et al. (1980) can be used for mortality estimates. The equations apply to upper and lower temperature ranges (Fig. 6) for temperature-induced mortality (M) from fertilization to part of the period when fish rise from the nest. Equations 4 and 5 apply to the 10° to 15° C and 27° to 30° C zones. No mortality would be expected for temperatures in the 15–27° C range.

$$M = 3.0 - 0.2 \ (T), \text{ if } 10 \le T \le 15 \qquad (4)$$

Table 6. *Estimates of days to hatching, days from hatching to fry rise, and days of postrise growth of young-of-year smallmouth bass at three alternative flow regimes. The average temperatures are hypothetical.*

	Alternative flow regime (cubic feet per second)		
	A 2,500	B 2,000	C 1,950
Temperature (and days to hatching)	15.6° C (6.8)[a]	17.8° C (4.8)	17.5° C (5.0)
Temperature (° C) during (and days in) hatch-rise interval	15.6° C (10.9)[b]	18.8° C (6.5)	18.8° C (6.5)
Total days from spawning to fry rise (and dates)	17.7 (5–23 May)	11.3 (5–16 May)	11.5 (5–17 May)
Days of growth (and mean temperature[c]) between fry rise and winter feeding cessation	138 (16° C)	168 (19° C)	136 (35° C)

[a] Days = $83.2e^{-0.1606T}$ = (83.2) (0.082) = 6.8.

[b] Days = $134e^{-0.1606T}$ = (134) (0.082) = 10.9.

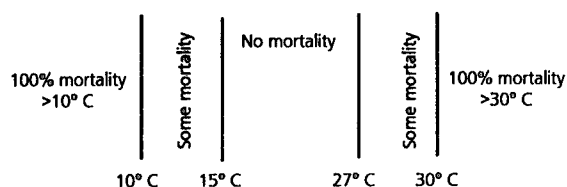[c] Mean water temperature in winter would approximate 10° C and lower, and growth would not occur.

Fig. 6. Thermally induced mortality for smallmouth bass eggs and fry in the temperate zone (from Shuter et al. 1980).

$$M = -9 + 0.33 \ (T), \ \text{if} \ 27 \le T \le 30 \qquad (5)$$

where

T = the average daily temperature (° C), and

M = level of total mortality for eggs over a period of time including that for fertilization to hatching and part of the hatch-to-rise period.

Equation 5 was used to develop data for a curve from which predicted mortality rates can be read for average daily temperatures in the 27 to 30° C range (Fig. 7). A similar curve could be developed with Equation 4 for the 10 to 15° C range. Based on estimated temperature data for the period that eggs, larvae, and fry would be present, the two equations could be used to estimate total mortality for alternative temperature regimes.
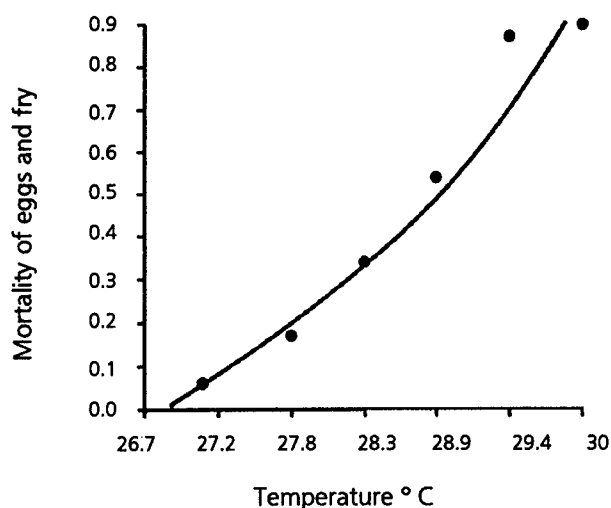
Estimating Prewinter Survival and Growth of Young-of-year Fish

Serns (1982) studied effects of temperature on survival of age 0 smallmouth bass in Wisconsin (Fig. 8). The number of young-of-year fish present in fall was positively correlated with spring and summer water temperatures. Seventy-four percent of the variability was attributed to summer water temperatures. Forbes (1981) also documented a correlation between higher water temperatures during the first growing season and year-class survival. Yields from a Lake Huron fishery correlated with the algebraic sum of monthly deviations of mean air temperatures from July through October of the hatching year (Fry and Watt 1957). In Oneida Lake, in New York, dominant year classes were related to above-normal mean June air temperatures (Forney 1972). There was no correlation between water temperatures and year-class strength at the end of the first summer in Katherine Lake in Michigan, but the opposite was true when postwinter year-class numbers were considered (Clady 1975). Although growth information was not discussed, the implication is that prewinter size attained during the first growing season determines winter survival because improved survival was documented following the June–October periods with the warmest
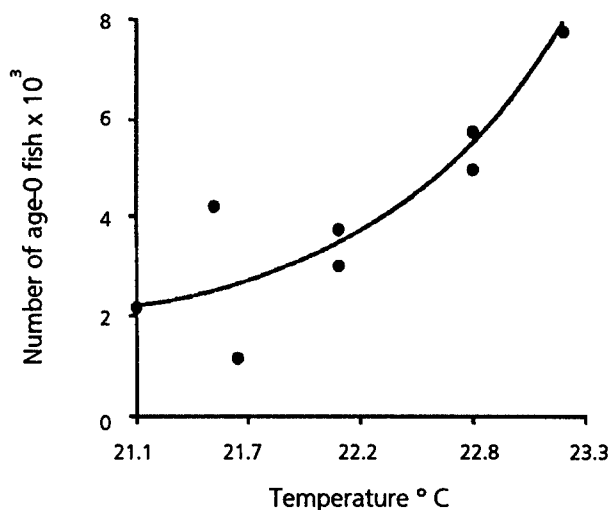

Fig. 7. Temperature versus mortality rate for smallmouth bass eggs, larvae, and fry (developed with equations from Shuter et al. 1980).

Fig. 8. Mean June through August water temperatures versus number of age 0 smallmouth bass the first fall of life (from Serns 1982).

temperatures. Christie and Regier (1973) hypothe-sized that the relation between temperature regime and its influences on the size of prewinter fish and their survival applies throughout the geographic range of smallmouth bass.

Shuter et al. (1980) studied effects of temperature on the first-year survival of smallmouth bass in Ontario. The two periods of vulnerability were the times from fertilization to nest abandonment by fry, and in winter, when the young fish were dependent on stored energy to survive. The study populations were north of the 45° N latitude, and I assume that the results would be similar for waters of the United States in which winter water temperatures approximate 7.2° C and lower.

Shuter et al. (1980) found an inverse relation between the time that fry rise from nests and winter survival rates of young-of-year fish, which is indicative of the importance of providing adequate time for growth before winter. There was a positive relation between the total length of young-of-year fish (Fig. 9) at the onset of winter and survival; their explanation was that larger fish store more energy, which is available for metabolism during the winter starvation period. The winter starvation period commences when water temperatures drop into the 7–10° C range (see Table 3). During this period, if fish energy stores are depleted and maintenance

requirements are not met, the result is winter mortality. Maintenance requirement energy is required for basic needs for survival including osmoregulation. Shuter et al. (1985) simulated effects of temperature changes in a thermal plume on smallmouth bass (Fig. 10). Mean survival of offspring on nests was related to the spawning date (Fig. 10A), and overwinter survival was dependent on total length by fall (Fig. 10B). MacLean et al. (1981) simulated temperature data for an Ontario lake and described the relation between the date of fry rise from the nests and average survival of young-of-year fish (Fig. 11).

Effects of low winter temperatures on the survival of young-of-year of different sizes was evaluated in aquaria for experimental regimes with endpoint temperatures ranging from 2 to 6° C (Oliver et al. 1979). Final winter temperatures did not affect survival, but there was a positive correlation between fish length and survival rate. There
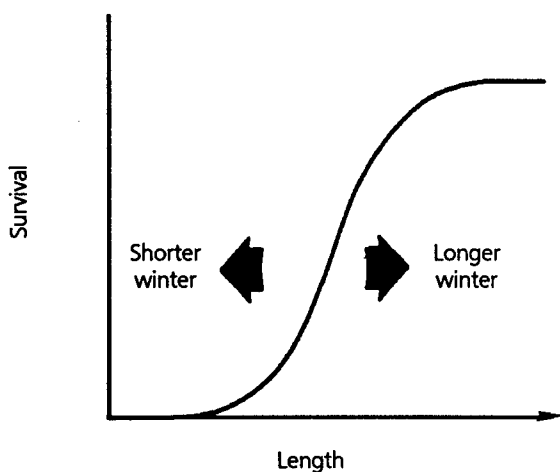

Fig. 9. Conceptual relation between overwinter survival of smallmouth bass and fish length at the end of the first growing season. The position of the curve is affected by the duration of the winter starvation period (from Shuter et al. 1980).
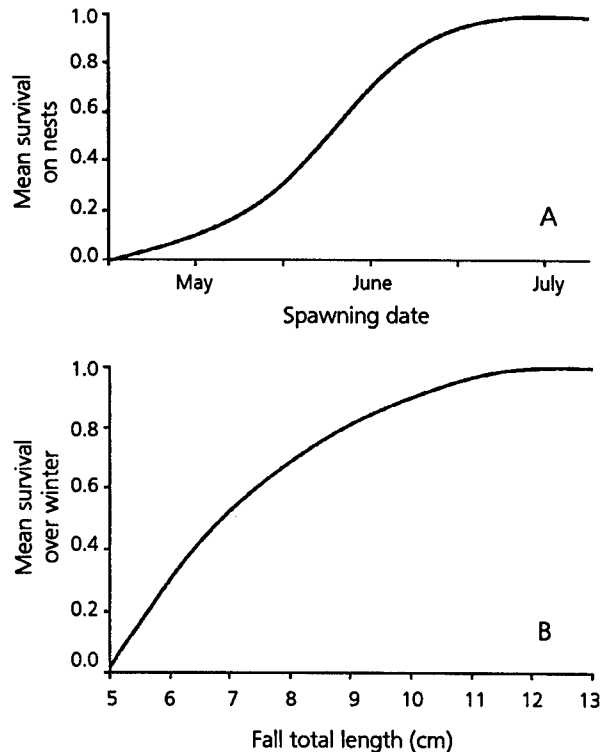

Fig. 10. Empirical relation between the spawning date and survival of young-of-year on nests (A), and fall total length and overwinter survival (B; from Shuter et al. 1985).
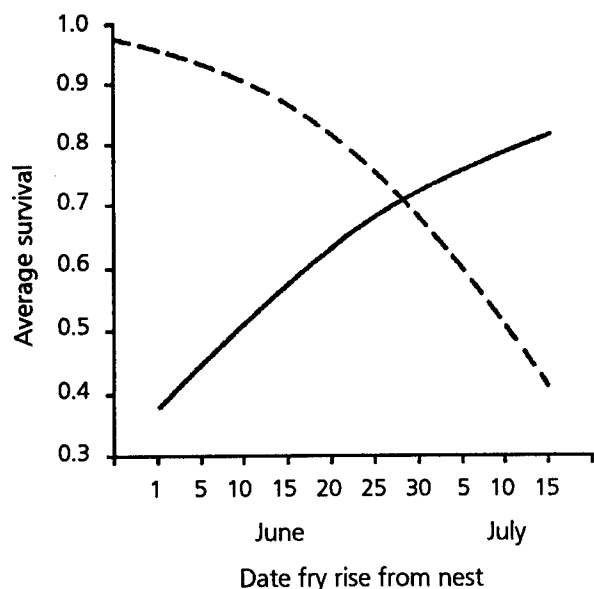
Fig. 11. Relation between the time that fry rise from nests and nest survival, time of rising, and winter survival. The *solid line* represents nest survival, and the *broken line* represents winter survival (from MacLean et al. 1981).

were no temperature-induced mortalities for fish in the 8.0 to 10.9-cm length class. Based on the study, hatchery workers were advised to stock "long" young-of-year fish to minimize first-winter mortalities.

The role of temperature in first-year survival of smallmouth bass was addressed by Shuter and Post (1991). They emphasized size of young-of-year fish at the outset of winter (Fig. 12). There is an inverse relation between fish size and basal mortality rate. When the starvation period is prolonged, stored energy is used sooner in smaller fish, to the extent that available energy is depleted enough to cause mortality. Thus, year-class success can depend on attainment of a minimum young-of-year size before the starvation period. Equations 6-9 (Shuter et al. 1980) can be used to estimate daily growth (G in centimeters per day) for estimating young-of-year prewinter lengths for a specified temperature (T).

$$G = 0.0 \text{ if } 14° \text{ C} > T > 35° \text{ C} \tag{6}$$

$$G = -0.17 + 0.012 \ T, \text{ if } 14° \text{ C} \le T < 25.5° \text{ C} \tag{7}$$

$$G = 0.14, \text{ if } 25.5° \text{ C} \le T < 31.5° \text{ C} \tag{8}$$

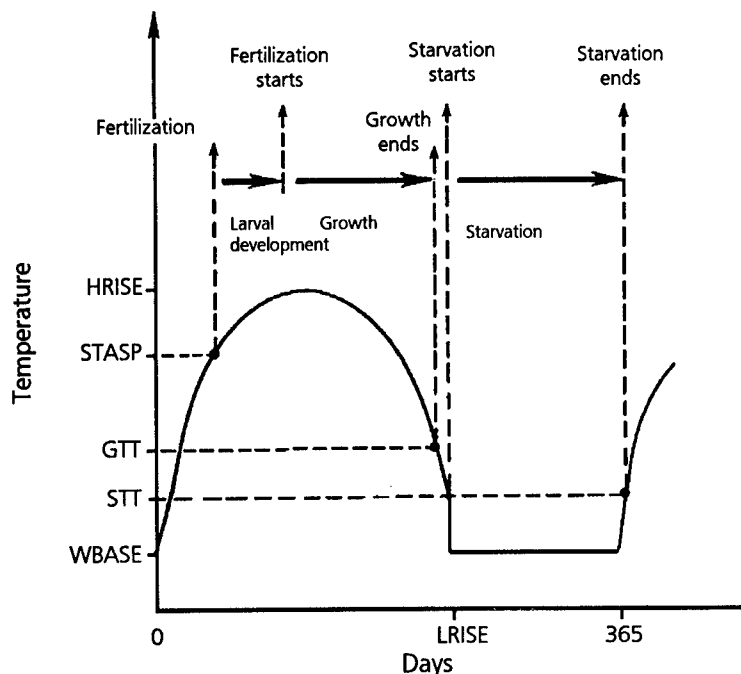$$G = 1.4 - 0.04 \ T, \text{ if } 31.5° \text{ C} \le T \le 35° \text{ C} \tag{9}$$

Fig. 12. The annual temperature cycle affecting smallmouth bass larval development, growth, and the winter starvation period. LRISE = days during a year in which the temperature exceeds the winter base temperature (WBASE), HRISE = maximum daily temperature during the year, STASP = temperature at which spawning first occurs during the spring rise, GTT = temperature above which somatic growth can occur, and STT = temperature below which starvation and decline in body weight occur (from Shuter and Post 1991).

where

T = the average temperature (° C) during the
course of a growing season when
temperatures are greater than 14° C but
less than 35° C.

An example of using the equations to evaluate
alternative temperature regimes is shown in
Table 7. The average temperature for the length
of the growing season must be estimated. If size
is designated as a limiting factor to overwinter
survival for a site, a decision must be made on the
minimum prewinter size. For example, if it is
agreed that the minimum acceptable size is 6 cm,
regime B is recommended (Table 7).

The size that should be attained by the onset of
winter depends on the number of days during the
starvation period. Lengths required for maximum
winter survival can be estimated with Fig. 13:
(1) estimate the number of days during the winter
starvation period (days when the average tempera-
ture is ≤10° C), (2) draw a vertical line that inter-
sects the L_0 and the L_1 lines, and (3) read the
lengths on the total length axis corresponding to
the points of intersection. For example, for
214 days, when the temperature would be ≤10° C,
L_0 = 4.5 compared with 8.5 for L_1. Based on energy

stores alone, the L_1 length is minimal for 100%
survival.

Horning and Pearson (1973) studied growth
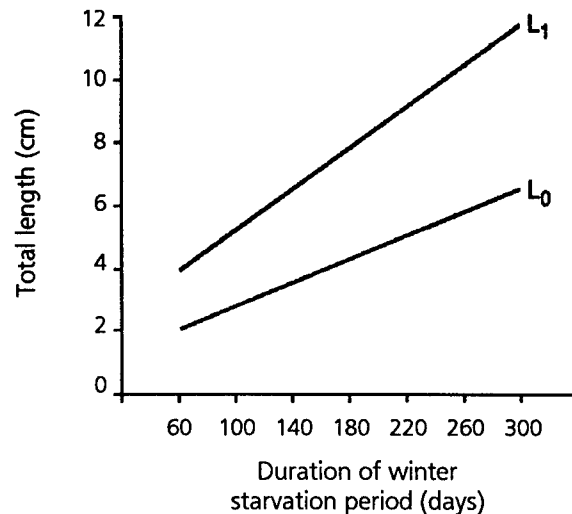rates of juvenile smallmouth bass at constant tem-

Fig. 13. Relation between duration of the winter
starvation period and lengths of young-of-year
smallmouth bass for two levels of survival. L_0 = the
maximum length for which overwinter survival is 0.0
and L_1 = the minimum length for which survival is 1.0
(from Shuter et al. 1980). See text for an example
using the graph.

Table 7. *Estimated lengths attained by young-of-year
smallmouth bass before the winter starvation
period for three temperature regimes. The mean
temperatures pertain to the hypothetical examples
in Table 6. It was assumed that the growing season
was 60 days and that fry were 1 cm (total length)
when they vacated the nest.*

	Alternative temperature regime		
	A	B	C
Mean temperature (° C)	16	19	35
Estimated total length (cm) by winter	3.8[a]	11.1[b]	1.0[c]

[a] Length = 1 cm + (138 days)(0.02 cm/day) = 3.8 cm
where 0.02 cm/day = G = -0.17 + 0.012T.

[b] Length = 1 cm + (168 days)(0.06 cm/day) = 11.1 cm
where 0.06 cm/day = G = -0.17 + .012T.

[c] Length = 1 cm + (136 days)(0 cm/day) = 1 cm
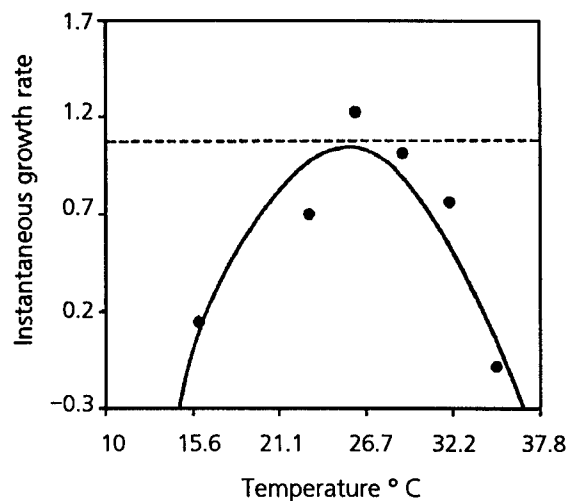where 0 cm/day = G = 1.4 - 0.04T.

Fig. 14. Relation of temperature and growth rate of
juvenile smallmouth bass (from Horning and Pearson
1973).

peratures ranging from 16 to 35° C. The highest instantaneous growth rate was 1.23 at 26° C compared with -0.08 at 35° C (Fig. 14). I assume that the maximum safe temperature of 29° C, which the authors recommended for growth, pertained to fingerling, juvenile, and adult smallmouth bass. The instantaneous growth rate information could be used to compare relative merits of alternative temperature regimes. The approach would be to estimate the average temperature for the growth period for a site and to assume that the regime with the highest growth rate would be preferred, provided that all daily maximum temperatures (not the means) would always be within tolerance limits for growth.

Estimating Effects of Sudden Temperature Drops on Juveniles

If temperature regimes have potential for sudden temperature drops, cold shock and mortality are possible. Equations 10 and 11 (Horning and Pearson 1973) can be used to estimate mortality of juvenile smallmouth bass for sites at which drops occur. The equations only apply to acclimation data within the 15–26° C range. Most mortalities reported for low temperature occurred within 24 h (Horning and Pearson 1973). Although responses to temperature are a function of exposure time, I assume that a short exposure (e.g., ≤ 1 h) would cause the same results from thermal shock.

$$Y = 0.74X - 9.71 \qquad (10)$$

Equation 10 provides the best fit when estimating the lower exposure temperature (Y) for TL_{50} mortality during a 1–7-day period following a low temperature event; X represents the acclimation temperature (° C).

For example, assume that the average acclimation temperature that preceded a sudden low temperature event is 15° C. Then $Y = 0.74 (15) - 9.71 = 1.39°$ C.

$$Y = 0.75X - 7.98 \qquad (11)$$

Equation 11 provides the best fit when estimating the exposure temperature (Y) for the predicted 96-h TL_{0-10} mortality following a low temperature event; X is the acclimation temperature (° C).

In Equation 11 the temperature at which the 96-h TL_{0-10} mortality would be predicted for an acclimation temperature of 15° C would = 0.75 (15) − 7.98 = 3.27° C.

The time required for acclimation to a given temperature regime is about 7 days (Wismer and Christie 1987). Therefore, when acclimation temperature information is required for Equations 10 and 11, estimation is necessary. One approach would be to assume that the average 7-day temperature that preceded a low temperature event is the acclimation temperature. This value could be specified as the average of the daily maximum and minimum temperatures.

General Considerations

I did not try to address all options for evaluating temperature regimes for protection of smallmouth bass. Instead, several concepts are offered for consideration by field biologists who must decide on approaches for site-specific applications. The following questions should be asked in all applications: Were accurate temperature data (simulated or estimated) used for existing and alternative regimes? Were experts qualified to work on temperature problems involved to attain agreement on appropriate temperature criteria? Was the rationale, including necessary assumptions, clearly documented to disclose the logic for the recommended temperature regime to be implemented? Were the results and recommendations reviewed by qualified experts, and was this step followed by corrective changes that were deemed technically justified?

Other questions to consider when evaluating the quality of simulated temperature regime information should include the following: Is information provided for important life history periods (e.g., spawning)? What is the basis for verifying that simulated temperatures for alternative regimes are accurate? One approach for answering the second question would be to verify that simulation data for previous studies were accurate, based on subsequent monitoring.

The accuracy of worst-case temperatures should receive special emphasis. Knowledge of these temperatures is important; lethal conditions can be a
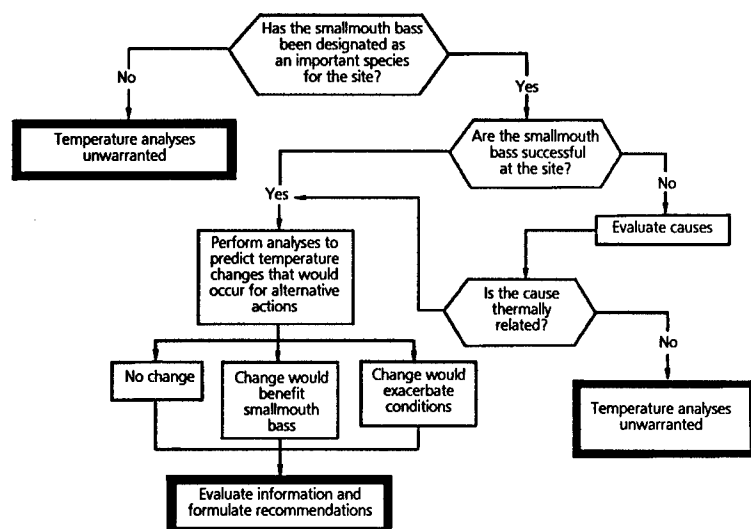
Has the smallmouth bass been designated as an important species for the site?

No

Temperature analyses unwarranted

Yes

Are the smallmouth bass successful at the site?

No

Yes

Evaluate causes

Perform analyses to predict temperature changes that would occur for alternative actions

Is the cause thermally related?

No

Temperature analyses unwarranted

No change

Change would benefit smallmouth bass

Change would exacerbate conditions

Evaluate information and formulate recommendations

Fig. 15. Flowchart for the temperature analysis process.

one-time event if tolerance levels are exceeded for an important life stage. Accordingly, the temperature range for all critical periods should be simulated for alternative regimes, although emphasis might be on daily mean temperatures for computations. For example, the recommended short-term maximum lethal temperature for incubating eggs is 23° C. Suppose that, for a hypothetical situation, the maximum temperature for 1 day during a hatching period was 25.6° C. Based on temperature-response data, this high temperature for 1 day would be lethal to all eggs. If only the mean temperature (e.g., 17.8° C) for the hatching period were considered, egg mortality would not have been predicted.

Another consideration is the relative growth rates of young-of-year fish. For example, fish require energy in flowing waters to hold position. Accordingly, there might be less energy available for young-of-year growth for a given temperature regime in flowing waters compared with laboratory experiments. Also, in laboratory experiments designed to study growth of young-of-year fish (and other stages), excess rations are usually provided; this condition probably would not exist in nature, which might result in lower growth rates than predicted.

I recommend conducting a preliminary evaluation before deciding that a temperature analysis is warranted (Fig. 15). Basically, three situations exist: smallmouth bass are present and successful,

they are absent, or they are present and marginally successful. If smallmouth bass are absent at a site and their establishment is being considered, an attempt should be made to agree on limiting factors, including physical and chemical habitat conditions. Reference information for a preliminary evaluation should include the Fish and Wildlife Service habitat suitability index publication on smallmouth bass (Edwards et al. 1983).

Existing adverse effects of temperature on specific life stages and activities should be documented including an inadequate prewinter growing period for age 0 fish, and intolerable temperature extremes for eggs, fry, or older fish. The purpose of documentation would be to emphasize improvements that might be necessary in a new temperature regime. A proactive approach would be to use the information to propose alternative regimes instead of waiting to respond to those proposed by a developer.

When evaluating alternative temperature regimes, ensure that indirect effects are considered and documented. As an example, suppose that spawning is delayed a month and that, from temperature data alone, it is predicted that young-of-year fish would attain an adequate size for winter survival. This assumption might be invalid because there is no guarantee that a new regime would result in synchronized abundance and size distributions (Adams et al. 1982) of food for young fish.

Acknowledgments

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